THE ANATOMY AND DEVELOPMENT OF SPIRORBIS BOREALIS.

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The following studies upon *Spirorbis* were made during the months of July and August at Woods Holl, Mass. This chaetopod annelid is found attached to the brown alga *Fucus* which grows on boulders and the piles of old wharves in the locality referred to. It is best collected at low tide and seems to limit itself to situations where there is a strong current. The food of the annelid worm consists of infusoria and minute forms of algæ.

From observations made during two summers, and upon material collected from eight localities in the region of Vineyard Sound and Buzzard's Bay, it appears that *S. borealis* has two breeding seasons. One of these extends from the middle of June to the middle of July; the other extends through the month of August. During the last two weeks of July no eggs were found either in the body cavity or in the shell. Examining egg-chains on July 6th, nothing but well developed embryos were found, while on July 31st, the very earliest stages of segmentation and undeveloped eggs were found in abundance.

The shape of the body of *S. borealis* is sub-cylindrical anteriorly, tapering posteriorly; there are two grooves, a ventral and a dorsal, in the latter is found the egg-chain. The outer segmentation corresponds to the inner, the number of metameres and dissepiments varying from 14 to 20. The segments are somewhat narrower on the ventral than on the dorsal side, probably due to the position assumed by the annelid in its shell. The external openings of the segmental organs or nephridia are found on the ventral side near the base of each metamere. On the prostomium are placed eight branchiæ, one of which is modified into an operculum. These branchiæ are branching and filiform, each branching portion being furnished with cilia arranged on either side. The branchiæ are arranged in a circum-oval manner. In the usual position of the annelid in the shell, the branchiæ and operculum only are protruded.

The eggs pass out through the operculum; its end bears a movable translucent plate of lime which protects the animal from

injury after it has withdrawn into its shell, which it does upon the slightest disturbance.

There are two body regions—thorax and abdomen. The prostomium and peristomium are not sharply separated from the succeeding metameres, but are coalesced into a buccal somite. The mouth is circular in form and is placed between two semicircular plate-like areas. The anus appears as a mere slit.

The metameres arise through a process of cell-division from the primitive layer of the undifferentiated mesoderm. The constriction of the metameres begins in the trochophore stage of the worm. The regions or layers of a metamere consist of the following: epithelium or ectoderm, body sac (taking the place of the solid primitive mesoderm), intestinal epithelium or endoderm and mesenchyme cells scattered between these layers.

The parapodia are slightly developed. The upper bear hair-like setæ; the lower consist of transverse ridges. In the adult worm there are three groups of falciform setæ placed on either side of the anterior thoracic region, each group containing from 6 to 12 setæ. These setæ arise from setigerous glands which are follicles formed from proliferation of the outer epithelial cells. Each seta is developed from one of several structural cells. In its growth it breaks through the follicle and extends from here over the surface of the surrounding epithelium. The follicle also projects into the body cavity and is furnished with muscle fibres.

Between the intestine and body-wall is found a cavity filled with fluid; this coelum or body cavity arises from the mesoderm by cleavage. It is divided into as many consecutive chambers as there are metameres (14 to 20).

In the alimentary system three divisions may be distinguished, fore-gut, mid-gut and hind-gut. The pharynx is non-protrusible. The fore-gut proceeds from the stomodeum of the larva and its epithelium is of ectodermal origin; it is very much reduced in size. The mid-gut is developed from the mesenteron of the larva; its epithelium is endodermal. This portion of the alimentary tract is the principal digesting portion, and presents two regions, the anterior or stomach intestine is wide, while the posterior is long and narrow. The hind-gut is short and is developed from the proctodeum of the larva.

The enteric canal is surrounded for its whole length by a blood sinus. Each branchial filament is penetrated by one blood vessel.

For the movement of the branchiæ there are well developed muscle groups. In the free swimming larva, and also in the adult form there are groups of muscles for the movement of setæ.

The egg-chain found in the dorsal furrow consists of from one to four rows, each containing from ten to fifteen eggs. The color of these eggs varies from brown to orange according to the stage of development. Each egg is enclosed in a capsule, while all the ova lie in a common membranous sac. The eggs are telolecithal with considerable nutritive yolk, as the larva does not leave the egg capsule until far developed.

The shell in its earliest formation is trumpet-shaped: later it gradually assumes the tightly coiled spiral form. As in all fixed forms, the body characters undergo considerable modification during development, and these are greatly influenced by the development of a limy covering. The shell gland is placed in the anterior-thoracic region, in the median ventral line.

S. borealis is hermaphroditic, the generative products arising in the walls of the perivisceral body cavity. The reproductive glands are arranged on either side of the intestinal canal near the stomach. Where the ova or sperm is developed is distinguished merely by the presence of the products. The eggs pass into the body cavity and from here into the operculum, where they are fertilized and a capsule secreted; from here they pass out through the opening of the operculum and are placed in the mid-dorsal furrow. The operculum of *S. borealis* does not serve for a brood-pouch as does that of *S. spirillum*.

DEVELOPMENT.

The unfertilized eggs are much smaller in size, have a paler color, and have a much more prominent nucleus than the fertilized eggs. The unsegmented egg has a brown color, the yolk is evenly distributed in large and small globules; the nucleus is very small.

The following table will serve to illustrate the usual length of time occupied by segmentation:—

	Unseg.	2-celled	4-celled	8-celled
(1)	11 A. M.	12 M.	1 P. M.	3.30 P. M.
(2)	11 A. M.	12 M.	1 P. M.	3.30 P. M.
(3)	11 A. M.	12 M.	1 P. M.	4.00 P. M.
(4)	11 A. M.	12 M.	1 P. M.	4.00 P. M.
(5)	11 A. M.	12 M.	1 P. M.	4.00 P. M.
(6)	11 A. M.	12 M.	1 P. M.	4.00 P. M.

All the eggs in the chain are never found to be in the same stage of segmentation. The following will show the typical arrangement: in a chain of 22 eggs, numbers 13, 18 and 20 were unsegmented; 2, 5, 6, 7, 9, 12 and 16 were 2-celled; 14, 3 and 4 were 3-celled; 1, 8, 15 and 22 were 4-celled; 10 was 5-celled. The observation was made at 2 P. M.; by 3 P. M. the successive changes had taken place in all these eggs with the exception of 13, 18, 20, 10 and 14, all of which were probably dead.

The segmentation in *S. borealis* is unequal. The first cleavage plane is equatorial, and takes place as the following will serve to illustrate:

11.00 A. M., egg unsegmented.
11.05 A. M., slight notch visible.
11.30 A. M., segmentation plane visible for one-half the circumference of the egg; polar globules present.
12 M., faint, but complete segmentation plane, 2-celled stage.
1 P. M., marked segmentation plane, resting period.

The egg having passed through the above described changes is now divided into two unequal portions, the smaller of which is ellipsoidal, giving the whole egg a somewhat dumb-bell shaped appearance. The capsule is distinct, but more closely approximated to the surface of the egg than in the preceding stage. There is no marked change in color, the lower larger cell is somewhat darker than the upper.

In the 3-celled stage the division plane passes upward through the smaller of the two cells already formed; this stage then consists of one large and two smaller unequal cells.

By continuation of the division plane of the last stage the lower and larger cell becomes divided into two unequal cells. This second segmentation plane is at right angles to the first or segmentation plane of the 2-celled stage. But by their peculiar intersection with each other, neither plane is any longer a continuous circle; the points of intersection are marked by *z*-shaped lines. The lower left cell is darker than the others, containing the most yolk. In segmentation of these eggs the first furrow or segmentation plane always bends to the right, the second bends to the left.

The next division takes place in a plane at right angles to the last. The first cell to be divided is the smallest of the four already existing cells; the polar globules take their position at the right hand side of this small cell. The general shape of the egg becomes modified somewhat at this stage. It is now irregularly spheroidal.

The successive stages up to the 16-celled stage are shown in the accompanying illustrations, Plate I. The origin of the respective cells is indicated by arrows. The cells of the 4-celled stage are designated A, B, C, D in the order of formation; A′, B′, C′, D′ are successively developed from these in the formation of 5-celled, 6-celled, 7-celled and 8-celled stages. In the same manner *a*, *b*, *c*, *d*, are derived from the previous A′, B′, C′, D′, forming stages 9-celled, 10-celled, 11-celled and 12-celled. The next four stages are designated *a′*, *b′*, *c′*, *d′*, and constitute 13-celled, 14-celled, 15-celled and 16-celled stages in their respective order of formation.

The blastula has a very small blastocoele; the blastopore forms the mouth. The cells of the endoderm take their origin from the macromeres of the lower half of the blastula, while those of the upper half give rise to the ectoderm. The mesoderm can be traced from the left posterior macromere. The blastula becomes bilaterally symmetrical by the rise of the primitive mesoderm cells; these lie in the posterior portion on either side of the median line. Next in development the endodermal cells of the blastula become invaginated into the segmentation cavity and form the archenteron, while the ectoderm grows over the invaginated portion. The primitive mesoderm cells sink between endoderm and ectoderm deeper into the segmentation cavity.

In the gastrula stage the blastophore is a median ventral, longitudinal slit; this closes from posterior to anterior until there remains only a small aperture. The first stage of the larva after segmentation almost entirely fills the egg capsule, and is surrounded by a zone of cilia. The body is opaque, reddish-brown in color, and flattened on one side just below the cilated zone.

In the second stage of the larva the ectoderm becoming invaginated, forms the stomodeum or larval oesophagus; the archenteron elongates backward. There is a central opaque yolk-mass which is surrounded by a layer of clear cells. This layer of clear cells is thickest on the same side that the larva of the previous stage was flattened. The zone of cilia persist and one pair of ocelli appear.

The third stage of the larva has the flattened portion of the body more marked than in the preceding stages. The collar originates as two prominent projections on the right and left of the ventral, posterior, median region of the body.

The prominent features of the fourth larval stage are the increase in the curve of the dorsal surface and the growth of the collar.

In the fifth stage the larva appears divided into three regions: anterior, middle and posterior. The anterior represents the cephalic region, and is separated from the middle by a ring of cilia. The collar coyers the whole ventral side of the middle body region; its entire surface is ciliated. The body is of an orange color, while the yolk mass is brown. There is a bright red projection below the collar in the ventral region. Two ocelli are visible.

The sixth larval stage is characterized by the greater development of the collar and the development of hook-like setæ in the lateral portions of the body; three pair of these setæ are arranged between the collar and the posterior portion of the larval body. The primitive body cavity lengthens during this stage. The region of body from the posterior portion to mouth, becomes flattened.

The body of the seventh larval stage is more vermiform; the middle body region being the largest. Four ocelli are present (the larger being the original two) which are placed on the apex of the prostomium in the median line. There is an apical tuft of cilia present and a ciliated post-oral ring. The mouth opens in the median, ventral line and has ciliated lips. The collar is ciliated and now covers only about one-third of the middle body region. The posterior portion of the body is narrower than the middle portion and is segmented; its surface is ciliated on the ventral side and there is a tuft of cilia on the last segment. The posterior end of the intestine opens on the dorsal surface of the last segment by means of an invagination of the ectoderm, and thus the anus is formed. The operculum develops during this stage, appearing as a narrow, triangular plate arising from the dorsal side of the head. The larva now releases itself from the egg capsule by pressing its spines against the walls, and becomes a free swimming form.

In the eighth stage of the larva the operculum increases in size; the ocelli which were first to appear, now disappear; the apical ocelli remain. The club-shaped tentacles are replaced by the beginning of branchiæ. The operculum continues to develop. The collar much reduced in size remains attached to the cephalic region. In the ventral portion of the same region is the shell gland represented by an oblong mass of cells. The larva ceases to swim about and sinks below the surface of the water, attaching itself to some object by means of a translucent limy secretion. This is the shell forming stage.

The formation of the shell was observed as follows: On July 29th at 8.30 P. M. the larva swam slowly about a limited area for about fifteen minutes. It then remained quiet and attached itself to the glass in which it had been placed, after a few minutes it began to secrete a translucent mass about it. At 9.30 P. M. the shell thus formed presented a translucent horn-shaped appearance and formed a permanent tube covering about one-half of the fully extended body. The upper half of the body was constantly protruded from and withdrawn into this half formed shell.

In the ninth stage the shell assumes a spiral form, but is about half the diameter of the adult shell. The annelid still possesses apical ocelli; the collar disappears; the tentacles are filiform and branched. By differentiation of the cephalic region, and by growth of the larva in length of the posterior part of the body, and by segmentation into numerous metameres, the originally unsegmented larva is transformed into the adult annelid.

The time occupied by the development of *S. borealis* from the first segmentation stage to that of the free swimming ciliated larva was found by a series of observations to occupy the space of three days. Two days later the annelids attached themselves and commenced the formation of shells; the length of time required from this stage on to completion of the adult shell has not been observed.

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EXPLANATION OF PLATES I AND II.

Figures 1 to 10. Segmentation stages.

Figure 11. Blastula stage.

Figure 12. Gastrula stage.

Figure 13. Sixth larval stage. Ventral view. (Still in the egg capsule).

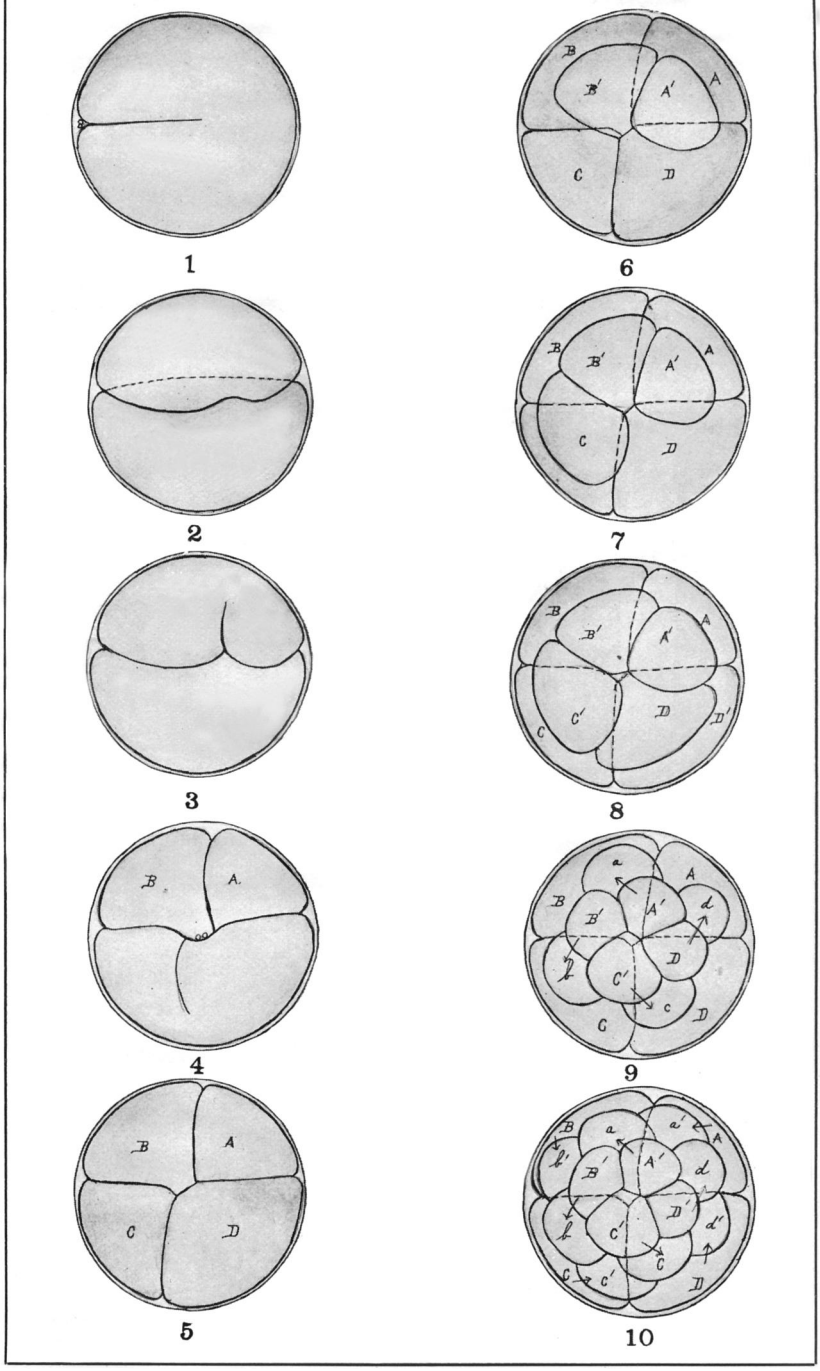
Figure 14. Seventh larval stage. Ventral view. (Ready to escape from egg capsule).

Figure 15. Early shell secreting stage. Ventral view.

Figure 16. Later shell secreting stage. Ventral view.

Figure 17. Adult *Spirorbis borealis* showing arrangement of branchiæ, operculum, alimentary tract, shell gland, generative glands.

Figure 18. Cephalic and anterior thoracic regions of adult *S. borealis* showing arrangement of branchiæ and operculum, groups of setæ, fore-gut of alimentary tract.



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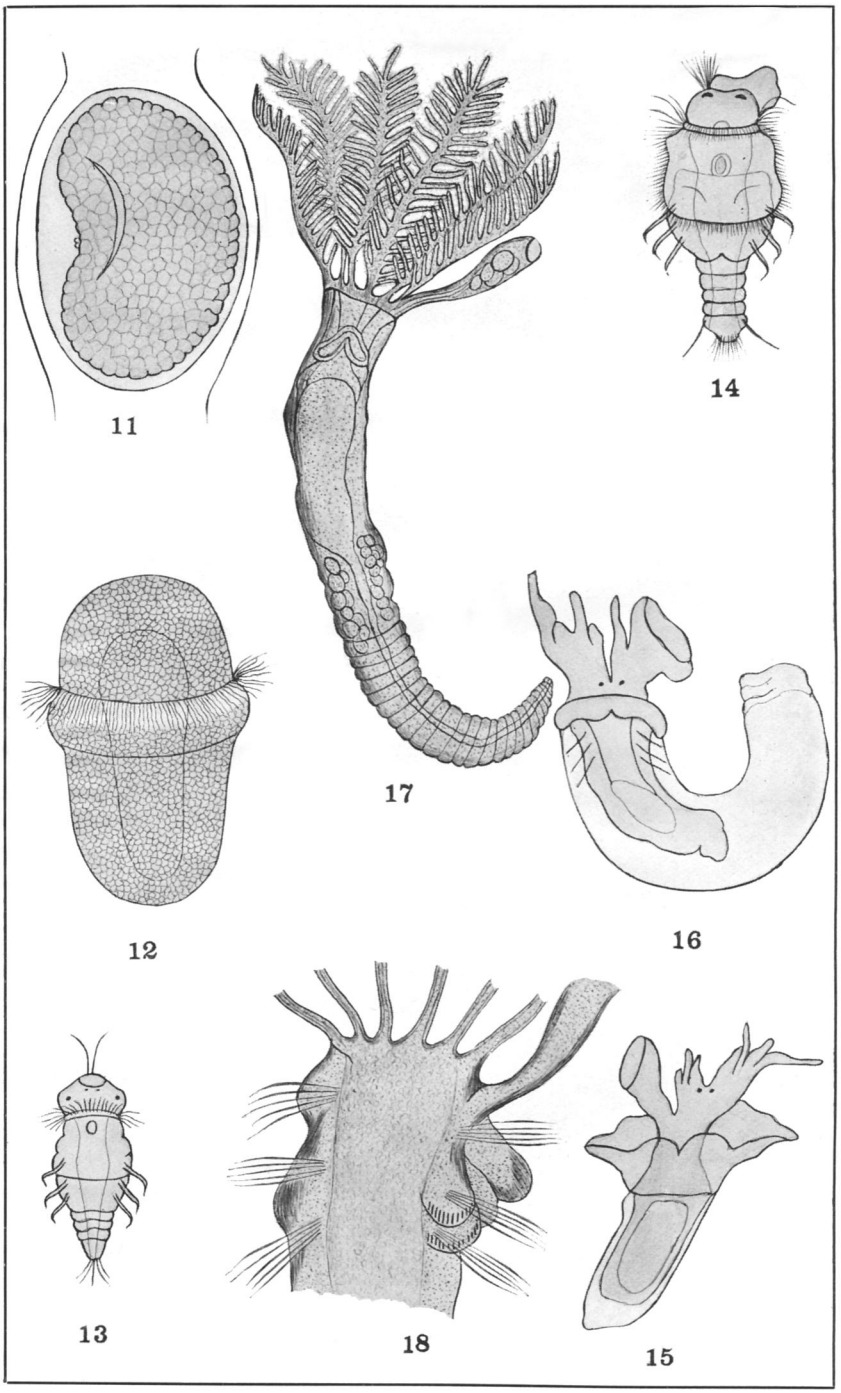

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